AN OVERVIEW OF THE DIOSPYROS CAMPECHIANA COMPLEX (EBENACEAE) AND DESCRIPTION OF THREE NEW SPECIES Mitchell C. Provance and Andrew C. Sanders UCR Herbarium Department of Botany and Plant Sciences University of California, Riverside Riverside, California 92521-0124, U.S.A.

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ABSTRACT

The *Diospyros campechiana* complex (Ebenaceae) is described in detail. Six species are recognized for the complex in Mesoamerica, and one species in South America. Expanded descriptions are provided for the three Mesoamerican species, and three new species are described. One new species, **Diospyros camposii**, is confined to a small region on the Pacific Slope of the Sierra Madre del Sur, Oaxaca, Mexico, while two others are known only from Costa Rica, including **Diospyros crotalaria**, which is restricted to the Osa Peninsula, and **Diospyros haberi**, which is widespread in mountainous regions. Members of the complex are remarkable for having fruiting pedicels that tend to hold fast to the calyx, despite being articulated to the receptacle. The fruit itself is weakly attached to the calyx. Photographs, comparison tables, and a key to the species of the complex are provided.

RESUMEN

Se describe en detalle el complejo *Diospyros campechiana* (Ebenaceae). Se reconocen seis especies en Mesoamerica, y una en Sur América. Se aportan descripciones en extenso para las tres especies Mesoamericanas, y se describen tres especies nuevas. Una de las especies nuevas, **Diospyros camposii**, está confinada a una pequeña región de la vertiente pacífica de la Sierra Madre del Sur, Oaxaca, México, mientras que otras dos se conocen sólo de Costa Rica, incluyendo **Diospyros crotalaria**, que está restringida a la Península de Osa, y **Diospyros haberi**, de las regiones montañosas. Los miembros del complejo son notables por tener pedicelos que, a pesar de estar articulados en el receptáculo, tienden a mantenerse firmes hasta el cáliz, mientras que el fruto está adherido débilmente. Las semillas se dispersan probablemente por pájaros. Se aportan fotografías, tablas comparativas, y una clave de especies del complejo.

While examining material during continuing studies of Mesoamerican *Diospyros* (e.g., Provance & Sanders 2005; Provance & Sanders 2006; Provance et al. 2008), building toward production of a comprehensive treatment of the Mexican species, three new taxa belonging to the *Diospyros campechiana* complex were discovered. Because this complex has only been discussed briefly (Provance et al. 2008), here we provide a more detailed account. The addition of three new species brings the number of included species to seven. One of the new species, *D. camposii*, is described from Oaxaca, Mexico, based on collections from a restricted area of the Pacific Slope of the Sierra Madre del Sur, and appears to be a local endemic. Two other species, including *D. crotalaria* and *D. haberi* are described for Costa Rica. *Diospyros crotalaria* appears to be a local endemic restricted to the Osa Peninsula, while *D. haberi* is fairly widespread in the central mountains. Previously described species include *D. campechiana* Lundell, *D. panamense* S. Knapp, *D. hartmanniana* S. Knapp, and *D. juruensis* A.C. Smith. The distribution of the complex extends from Oaxaca and Veracruz, Mexico southward to Panama, and likely enters Columbia, since *D. panamense* has been collected very close to its border. The complex definitely occurs in South America because *D. juruensis* occurs in the Jurua River Basin of the Amazon watershed in western Brazil, where the only known collection was made.

We are unsure about the complete status of this complex in South America because most South American specimens are unavailable for examination. In addition, the protologs of twenty-five recently described species of South American *Diospyros* (Wallnöfer 1999, 2000, 2003, 2005) completely lack photos or other illustrations, and are devoid of comparisons to allied, or even similar-looking taxa. This makes many of them difficult or impossible to place with confidence. Identification keys were also not provided, and no attempt was made to fit them into existing keys (e.g., MacBride 1959; Cavalcante 1963a; White 1981; Sothers & Berry 1998). While not violations of the International Code of Botanical Nomenclature (Greuter

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et al. 1994 2000), the figure omissions are inconsistent with Recommendation 32B, and the omission of comparisons to allied taxa is contrary to Recommendation 32C of the Code. Comparisons among taxa are made in virtually all of the other relevant literature (e.g., Miquel 1856; Hiern 1872; Milbraed 1927; Gleason & Smith 1933; Sandwith 1931, 1949, 1963; MacBride 1959; Cavalcante 1963a, 1963b, 1966, 1977; White 1981; Sothers & Berry 1998; Sothers 2003), and the illustration of types has been standard procedure for most modern taxonomists. Consequently, a more thorough examination of South American specimens may reveal that additional members of the D. campechiana complex are present there. However, our examination of the literature and the limited South American Diospyros specimens to which we have had access did not reveal any other such species.

The species in this complex are so poorly represented in herbaria that from over fifty herbaria that provided specimens of Diospyros, we received only seventy-three specimens (representing fifty collection events) that were referable to species in it. Little or nothing has been recorded concerning bark texture and color, color of the slash, wood characteristics, fruit color, texture and taste, flower odor, and color of the seeds and guard cells in life for most species. Flowers are completely unknown in D. camposii and D. crotalaria, and male flowers are known from only one or a few collections in the other species. Specimens with female flowers are especially rare: we have seen open female flowers only in D. campechiana, and only a single female flower bud in D. haberi. Regardless of sex, flowering specimens typically have few open flowers. Fruits seem to be unknown in D. juruensis.

METHODS

All of the relevant literature and specimens, including those types we could obtain, were evaluated. Collections were sorted into preliminary groups based on qualitative and quantitative morphological characters, and these groups were considered taxonomic hypotheses warranting continued investigation. Comparisons were then made between specimens assigned to each group and type specimens, specimens determined to be consistent with a species protologue (especially if from near the type locality) and paratypes determined to be consistent with the original description. We also examined specimens in light of floristic and monographic treatments, and the annotations of previous workers. Expanded descriptions have been constructed for previously described species based on the studied herbarium specimens. In this treatment we use 'lanceolate' in the sense of Jackson (1916), being broadest near the lower third of the leaf, not at mid-leaf in the sense of Stearn (2000). Descriptions apply to herbarium material except when indicated, or when obviously referring to fresh material. Map coordinates geo-referenced by the authors are given in brackets. Distribution maps were constructed using The Generic Mapping Tools 4.1.4 (Wessel and Smith 2006) accessed through OMC (Weinelt 2006) and amended using Adobe Photoshop (Ver. CS 8.0, Adobe Systems Incorporated, San Jose, CA). Illustrations are by the first author.

TAXONOMIC TREATMENT

Diospyros campechiana complex: Members of the Diospyros campechiana complex are evergreen trees with medium to large, more or less evenly spaced leaves. Petioles and midribs are occasionally transversely fissured, and frequently have a bloom of minute white crystals (scintillae) that are probably derived from cuticular wax, though their origin has not been studied. Stems and leaves are glabrous to sparsely hairy, and members of the complex have been variously referred to as "black strigillose," in reference to D. campechiana (Standley & Williams 1967), or "minutely strigillose" in reference to D. hartmanniana (White 1978). At low magnification the vestiture appears to be comprised of minute, mostly black, appressed, fusiform hairs. At higher magnification it becomes evident that most hairs are dark red and 2-armed, with a short basiscopic arm, and a longer acroscopic arm. Less often hairs are simple, and in some species there may be a high frequency of similar, but paler, yellowish, or reddish brown hairs. In addition, some taxa are minutely hirtellous or minutely pubescent, with hairs much smaller than those of the aforementioned strigillose vestiture. Stems sometimes have localized patches of atypical hairs (e.g., upright, aspergilliform, etc.) which

we think represent endophytic fungi. In this paper the term "strigillose" refers to the common vestiture of dark red to black, simple and 2-armed hairs, with the addition of modifiers for special cases (e.g., "reddish brown strigillose").

The abaxial lamina surfaces typically have some conspicuously darkened guard cells (Fig. 1), and in all species except *D. campechiana*, the stomatal apparatus is recessed, giving the epidermis a black-puncticulate appearance at 20× magnification. The black dots on the abaxial lamina surface of *D. hartmanniana* that were interpreted by S. Knapp (1997) to be the bases of broken hairs may have been these pigmented guard cells. We suspect that darkening of guard cells is a result of secondary compound degradation in non-functioning cells of older leaves.

Male inflorescences are (1-)2-23(-29)-flowered glomerules, compact cymes, paniculiform cymes, or occasionally fasciculate cymes, in leaf axils of young stems. Their axes are 4-angled, and more densely hairy than leaves and stems, though the hairs are otherwise similar. Female inflorescences are solitary or 2-5(-10)-flowered cymes in leaf axils of young stems, and often more or less 4-angled.

Flowers have 4–5 calyx and corolla lobes, though rarely a calyx or corolla will have only 3 lobes. Corollas are urceolate and white in life, though they turn dark brown upon drying. Male flowers have 10–28 stamens with their filaments fused into 5–14 pairs (comprised of an inner and outer member). Filaments are adnate to the base of the corolla or inserted on the receptacle. Filaments and/or anther connectives are sericeous. The apex of the anther is tapered to rostrate, and consists mostly of minutely muricate connective tissue. The pistillode in male flowers is markedly lobed, with the number of lobes being equal to, or slightly less than, the number of stamen pairs surrounding it. In *D. campechiana* the filaments of adjacent stamen pairs are separated by these lobes, and in *D. panamense* and *D. hartmanniana* the indentations between the lobes resemble impressions of the filaments, suggesting that pressure from filaments against the pistillode during floral development may be responsible for the lobe pattern on the pistillode. Female flowers in *D. campechiana* possess eight unpaired staminodes, with several short hairs on the

abaxial surface of the connective, and lanceolate antherodes with slits. Open female flowers and their internal structures have only been observed in this complex in this one species, though a single mature flower bud has been observed in *D. haberi*. Despite female flowers being largely unknown in the complex, styles often persist on fruits, and their number (1–2) and morphology are useful in species identification.

The female calyx accresces during enlargement of the developing fruit, though not as markedly as in members of the *D. rosei* complex. The fruiting calyx tube is patent ("saucer-shaped" sensu White 1978; Knapp 1997) with a short basal protuberance. The apex of the fruiting pedicel is 4-angled, ± pyramidal in shape, and is jointed to the receptacle within the protuberance at the base of the calyx. Although *Diospyros* is typically described as having fruits with a persistent calyx (e.g., Wallnöfer 2001), members of the *campechiana* complex have a fruit that is weakly attached to the calyx. Despite having a pedicel with an articulated apex (as in other *Diospyros* species), in members of this group the fruit often detaches from the calyx, while the connection of the pedicel apex to the base of the calyx holds firm.

The fruits of members of the complex are small to medium-sized, ovoid-ellipsoid or depressed-globose to subglobose, and reportedly green, yellow, orange, or red when mature. Comparing fruit shape between species is not straightforward, since it is highly influenced by the number of seeds that develop. Fruits are usually asymmetric (e.g., Figs. 4b, 6b) when seeds only develop on one side. The fruits have only a small amount of flesh, which is reddish and vitreous when dry, though possibly viscous and clear in life. There are 1–4 locules separated by complete septa in the taxa in which fruit anatomy was studied. Based on fruit lobes, this also seems to be the case in the remaining taxa. Each locule contains a lone seed which lacks adherent pericarp. The large locules include considerable space around the seeds, and when dry fruits are shaken they produce a rattling sound.

The combination of brightly colored small to medium-sized fruits, that readily separate from the calyx, and contrasting black or very dark inflorescence branches, suggests avian seed dispersal in the complex. We suspect that dispersal in the *campechiana* complex is effected by removal of the fruit from the calyx,



FIG. 1. Epidermis details in species of the *Diospyros campechiana* complex. **A.** Abaxial leaf surface of *D. camposii* (scale = 0.5 mm) from *A. Campos V. & R. Torres C. 825* (MO). **B.** Abaxial leaf surface of *D. crotalaria* (scale = 0.5 mm) from *R. Aguilar 2877* (K). **C.** Pigmented and non-pigmented guard cells on the abaxial leaf surface of *D. hartmanniana* (scale = 0.125 mm) from *G. McPherson & N. Hensold 15310* (B-100152291). **D.** Pigmented and non-pigmented guard cells on the abaxial leaf surface of *D. crotalaria* (scale = 0.25 mm) from *R. Aguilar 2877* (K).

and swallowing of the fruit whole, unlike in other groups (e.g., the *salicifolia* complex), where fruits are torn open and seeds are swallowed incidentally along with adherent pericarp (White 1978; Provance pers. obs.). Alternatively, the combination of detachment of the fruit from the calyx and air space surrounding seeds in mature fruit may suggest a hydrochorous dispersal syndrome (Kubitzki & Ziburski 1994).

Diospyros campechiana Lundell, Contr. Univ. Michigan Herb. 4:23. 1940. (**Fig. 2, 3, 15b**). Type: MEXICO. CAMPECHE: Palizada, [18° 15'N, 92° 05'W, 3 m], 25–28 Jul 1939, *E. Matuda* 3843 (HOLOTYPE: MICH; ISOTYPES: F, K!).

Trees 6–20 m tall, evergreen; trunk up to 45 cm dbh, bark unknown, latex reportedly yellow to orange; young stems smooth to shallowly furrowed, brownish, usually dark, viscid, sparsely to moderately strigillose, also densely hirtellous, the hairs minute, light gray to ± colorless, shorter than the appressed hairs; mature stems lenticellate, glabrate. Leaves alternate, simple, entire; petioles 6–17 mm long, minutely hirtellous, sometimes with a few transverse fissures, rounded below, the epidermis longitudinally wrinkled, often scintillant, ± flat above, somewhat canaliculate distally; lamina subcoriaceous, oblong-lanceolate to oblong-elliptic, sometimes oblong-oblanceolate, 100–285 mm long, 35–90 mm wide, length to width ratio ca. 2.1–3.5: 1, base acute to attenuate, sometimes tapering, usually decurrent on the petiole, margin revolute, apex acuminate with a rounded tip; lower lamina surface dull brown, glabrescent to strigillose, guard cells sometimes conspicuously darkened, but not recessed; upper lamina surface dull brown to somewhat glossy, usually papillose. Venation eucamptodromous to camptodromous; midrib + rounded below, longitudinally wrinkled, depressed above, sparingly and minutely hirtellous and strigillose near the base of the lamina; lateral veins 7–12 per side, prominent below, slightly raised above; 3° veins slightly raised below, more so above. Laminar extrafloral nectaries on the abaxial surface only, common, round to elliptic, 0.3–0.5 mm long, minutely rimmed, drying dark green to black. Male inflorescences a single (3–)6–23(–29)-flowered compound cyme in the leaf axil of young stems (sometimes bordering on being a fascicle of 2(–3) cymes), 5–17(–31) mm long, initially paniculiform, but the terminal and often the penultimate units dichasia, axes 4-angled, densely strigillose, also minutely hirtellous, sulcate, subtended by ovate to triangular, concave bracts ± 1 mm long; peduncles 1.5–5.5 mm long; pedicels 0–1.5 mm long. Male flowering calyx subcrateriform (urceolate prior to anthesis), with a short basal protuberance, exterior drying dark brown to black, strigillose, papillate, interior glabrate to locally strigillose, 2–2.4 mm wide, tube ± 0.7 mm long, lobes 4-5, depressed-orbicular to widely ovate, 0.8-1 mm long, 0.8-1.4 mm wide, sometimes emarginate, often slightly asymmetric, suberect; male corolla white in life, drying brown, glabrous except for some minute papillae, tube urceolate, 1.2–1.7 mm long, ± 2.3 mm wide, lobes (3–)4(–5), 1–1.6 mm long, 1.4–1.9 mm wide, depressed-orbicular to widely ovate, sometimes emarginate, often slightly asymmetric; stamens (12–)16(–20?), with Whitefoord and Knapp (1998–onward) reporting 12–16 stamens and Pacheco (1981) reporting 16 stamens, these inserted on the receptacle, fused near the base of their filaments into (6-)8(-10?)pairs, the outer stamen larger, bowing inward at the middle, anthers yellow, sometimes with minute red spots, lanceolate, outer anthers 1–1.2 mm long (including the connective), sericeous on the abaxial surface along the connective and sometimes on the adaxial surface, hairs yellow to reddish black, inner anthers similar except smaller, less hairy, and the hairs mostly on the adaxial surface, the apex (connective) tapered, minutely muricate, filaments 0.2–0.8 mm long, sericeous near the base of the anther; pistillode rotate, markedly 8(–10)-lobed, 0.7–1 mm wide, glabrous, with 2(–1) broadly rostrate apical structures. Female inflorescences 1–3 compound cymes in leaf axils on young stems, paniculiform, but the terminal units dichasia, (1-)3-5(-10)-flowered, though no more than three fruit seen on a single inflorescence, 5-8 mm long, axes 4-angled, strigillose, also minutely hirtellous, sulcate, subtended by persistent bracts similar to those of male inflorescences; flowering peduncles 0.5–2 mm long; flowering pedicels 0.5–2 mm long; fruiting peduncles 4–6 mm long; fruiting pedicels 2–5 mm long, with a 0.4–0.5 mm long, 4-angled, pyramidal apex, only the distal 0.2–0.3 mm forming a joint within the basal protuberance of the calyx. Female flowering calyx campanulate-infundibuliform to crateriform (urceolate prior to anthesis), with a short basal protuberance, exterior drying dark brown to black, moderately strigillose, minutely papillate, ca. 2.5 mm wide, **tube** 1.2–1.5 mm long, **lobes** 4–5, depressed orbicular, (1.1–)1.7–1.9 mm long, 1.5–2.5 mm



Fig. 2. Diospyros campechiana. A. Fruiting stems (C.L. Lundell 17840, F). B. Stamens and pistillode (C.L. Lundell 20739, MO). C. Inflorescences with persisting calyces. (C.L. Lundell 17840, F).



Fig. 3. Diospyros campechiana. A. Male flower (C.L. Lundell & E. Contreras 20739, MO). B. Pistillode (C.L. Lundell & E. Contreras 20739, MO). C. Female flower (L. Pacheco & J.I. Calzada 20, XAL). D. Female flower (L. Pacheco & J.I. Calzada 20, XAL).

wide, erect; female flowering corolla white in life, drying brown, tube 0.9 mm long, 1.3-1.5 mm wide, slightly constricted distally, throat 1.2 mm long, semiglobose to urceolate, 2.3–2.5 mm wide, lobes 4–5, widely ovate, 1.7–1.9 mm long, ca. 1.6 mm wide, erect (L. Pacheco & J.I. Calzada 20) or spreading slightly (W.E. Harmon & J.A. Fuentes 5790); pistil ± globose, glabrous; style 1-2.1 mm long, glabrous, the basal portion 4-angled, divided from the basal 1/3 to 1/2 into two ascending branches (style and stigma [see below] details based on those seen in flowering material and persisting on fruit); stigmas minute, undulating irregularly along the abaxial perimeter of the style branches; staminodes 8, with several short hairs on the abaxial surface of the connective, antherodes lanceolate, with slits. Fruiting calyx not markedly accrescent, relatively thin (not fleshy), drying very dark, exterior glabrate to strigillose, minutely glandular punctate (punctae developing from the minute papillae of flowers), tube patent, with a basal protuberance 0.8–2 mm long and 1.5–2 mm wide, the tube 3.5–6 mm wide between opposing sinuses, interior glabrate to moderately strigillose, sometimes minutely glandular punctate, scattered clavate glandular hairs sometimes present, a circular band of short reddish black hairs sometimes present at the base, lobes spreading, (2_)2.5_4 mm long, (3_)4_5(-6) mm wide, depressed orbicular, margins repand, sometimes partly revolute, ciliate, adaxial surface glabrate to moderately strigillose. Fruit glabrous, (10–)13–17 mm long, 10–17 mm wide, ovoid-ellipsoid, often asymmetric, locules 1–4, separated by complete septa; flesh sparse to negligible, red and vitreous when dry, unknown in life, though likely viscous and clear; epidermis probably smooth in life, usually wrinkled when dry, color progressing from green to yellow to orange with maturity (rarely reported to be red), orange to dark brown when dry; seeds 1–4, reddish brown to brown, loosely contained in the fruit, ovoid to ellipsoid, the shape depending on the number of seeds that develop, circular in x.s (when one seed develops), or with 1–2 flat surfaces (when 2–4 seeds develop), 9.5–12 mm long, 5.7–8.4 mm wide, the dorsal surface with a prominent vascular strand, texture rugulose-foveolate, hilum apical on a minute protuberance.

Diospyros campechiana is probably most closely related to D. camposii. Separation of these taxa is discussed under the description of the latter. Generally, D. campechiana is an easy species to identify. In addition to the geographical separation of this species from other members of the complex, the narrow oblong leaves are distinct, being reminiscent only of D. crotalaria. However, the minutely hirtellous vestiture of the stems, petioles, midrib, and inflorescence seems to be diagnostic. Fruits in fragment folders that have retained their calyx often have the broken tip of the pedicel apex lodged inside the protuberance of the calyx. Thus, in many cases, fruits and calyces that broke away as a unit during the collection process, did not separate from the mother plant at the point of articulation of the pedicel and receptacle/calyx, but rather the pedicel broke near the opening of the cavity in the protuberance at the base of the calyx.

It seems likely that pressure from filaments during floral development creates the lobed pattern on the pistillodes of species in this complex. Because we observed mostly 8-lobed pistillodes in this species, we surmise that the stamen number is usually about 16.

Distribution and ecology.—Diospyros campechiana occurs in lowland tropical forests associated with wetlands and riparian areas of major river systems and their tributaries between sea-level and 270 m elevation in the states of Tabasco, Campeche, Chiapas, and Veracruz, Mexico, and Guatemala (Fig. 5).

Specimens examined. MEXICO. CAMPECHE. Mpio. Palizada: 20 km de Palizada hacia el entronque a Escárcega, 18° 07' 19"N, 92° 07' 15"W, [0-4 m], 2 Dec 2000, P. Sima et al. 2555 (MO). CHIAPAS. Mpio. Ocosingo: a 3 km al S de Frontera Corozal, paralelo a Río Usumacinta, selva alta perennifolia, [near 16° 49'N, 90° 53'W], 120 m, 17 Aug 1984, E. Martínez S. 7326 (CHAPA). TABASCO: "Habitat ad margins fluvii Gonzalez," [18° 15'N, 92° 55'W, 10 m], 8 May 1889, J.N. Rovirosa 482 (K). Mpio Jalapa: 4 km de la desviación carretera Xalapa-Tacotalpa, potrero, [near 17° 50'N, 92° 48'W], 10 m, 22 Nov 1983, F. Ventura A. 20785 (MO, XAL); Mpio. Comalcalco, San Cayetano, potrero, [18° 22'N, 93° 13'W], 0 m, F. Ventura A. 20796 (MO, XAL). Mpio. Jalapa-Tacotalpa: en el cerco de un potrero, 10 m, 23 Nov 1983, R. Curiel A. & M.A. Guadarrama O. 108 (CHAPA, XAL). Mpio. Macuspana: 8 km de la entrada de Macuspana hacia Escarcega y 1.5 km al N, selva inundable, asociado con Pachira, Bactris, [near 17° 41'N, 92° 34'W, 45 m], 25 Aug 1981, M.A. Magaña A. & S. Zamudio 358 (XAL). Mpio Nacajuca: Tucta, a 2 km de Incunac, selva median caducifolia, 2°, suelo cafe super-arcilloso anegado, [18° 12'N, 92° 59'W], 26 m, 6 Oct 1978, J.I. Calzada 4906 (XAL). Veracruz. Mpio. Ignacio de la Llave: [probably the town of Ignacio de la Llave], acahual, [18° 43'N, 95° 58'W], 50 m, 13 Nov 1967, G. Martínez C. 1555 (USF); 500 m de donde empieza la desviacion Villa Nueva–Zacate Colorado,

en potrero, 18° 43'N, 95° 59'W, 50 m, 29 Apr 1981, *L. Pacheco & J.I. Calzada 20, 21* (XAL). **Mpio. Las Choapas:** Las Choapas, orillas del Rio Playas, cerca de Abasal (one sheet indicates "Rio Playas, arriba de Abasal"), [near 17° 45'N, 93° 57'W], 30 m, 4 Aug 1984, *Miguel Chazaro & Luis Robles 3081* (XAL-2 sheets). **GUATEMALA. ALTA VERAPAZ:** Sebol, along Rio Sebol, in high forest, [15° 48'N, 89° 57', 153 m], Aug 1964, *Elias Contreras 5354* (F, MO); Sebol and vicinity, [15° 48'N, 89° 57', 153 m], Aug 1964, *Elias Contreras 5354* (F, MO); Sebol and vicinity, [15° 48'N, 89° 34'N], 29 Oct 1968, *Elias Contreras 8032* (F, MO). **PETEN:** La Cumbre, km 142 of Cadenas Road, in low forest on wet land, [16° 05'N, 89° 31'N], 29 Oct 1968, *Elias Contreras 6220* (F); Rio Pasion, Altar de Sacrificios, in high forest on bank of river, [16° 30'N, 90° 32'W, ± 380 ft], 8 Feb 1964, *C.L. Lundell 17840* (F, IJ, MO); El Rosario, the FAO-FYDEP Camp at Sayaxche, from thickets along small laguna, [16° 31'N, 90° 10'W], 160 m, 19 Jun 1971, *W.E. Harmon & J.A. Fuentes 5790* (UMO); La Cumbre, caserio "Sapurul", bordering arroyo "Sapurul", in zapotal [and] high forest, [near 16° 05'N, 89° 21'W, 270 m], 7 April 1977, *C.L. Lundell & Elias Contreras 20739* (WIS, MO); La Cumbre, Pusila Road, 5 km N, in acahual, [16° 07'N,

89° 21'W, 250 m], 19 Aug 1976, C.L. Lundell & Elias Contreras 20224 (MO, UCR); Brecha Chinajá, 12 km from Laguna Petexbatun, high forest, [16° 18'N, 90° 08'W, 540 ft], 20 May 1965, Elias Contreras 5401 (MO).

Diospyros camposii M.C. Provance & A.C. Sanders, sp. nov. (Figs. 1a, 4, 15c). Type: MEXICO. OAXACA. Mpio. San Jerónimo Coatlán: 41.5 km al SW de San Jerónimo C. [Coatlán], brecha a Progreso, bosque de pino-encino alterado, suelo amarillo arcilloso, 16° 10'N, 96° 59'W, 1550 m, 29 Nov 1990, *A. Campos V. 3452* (HOLOTYPE: CHAPA!; ISOTYPE: MEXU).

Arbor *D. campechiana* Lundell similis, sed fructu longiore, calyce fructifere crassiore, intervallo grandiore inter sinos oppositos, lobis longioribus et reflexissibus in fructibus, et stylo apicoque fructus pilosibus, caulibus, petiolis, costa inflorescentibusque non hirtellis, lamina breviore et marginis minute porcatis, sed non revolutis, differt.

Trees 8–25 m tall, probably evergreen; trunk unknown; stems brownish, shallowly furrowed when young, sometimes smooth, sparsely strigillose, becoming lenticellate and scaly in older stems. Leaves alternate, simple, entire; petioles 8–14 mm long, with a short marginal wing distally, sometimes transversely fissured, sparsely strigillose, epidermis scintillant; rounded below, epidermis longitudinally wrinkled, ± flat above, somewhat canaliculate distally; lamina chartaceous to subcoriaceous, widely ovate to elliptic, 55–152 mm long, 33–69 mm wide, length to width ratio ca. 1.5–2.5: 1, base acute to shortly-attenuate, sometimes oblique, decurrent on the petiole, margin minutely ridged, apex acuminate with a rounded tip; lower lamina surface dull brown, sparsely strigillose, the hairs densest near the leaf base, many guard cells darkened and often recessed; **upper lamina surface** dull brown, slightly paler than the lower surface, smooth, glabrous. Venation camptodromous to eucamptodromous; midrib subprominent below, ± rounded, sparsely strigillose, the epidermis longitudinally wrinkled, somewhat raised above with a narrow central canal, glabrous; lateral veins (5–)6–9(–11) per side, fine, but prominently raised below, flush or slightly raised above; 3° veins fine, conspicuously raised below, barely raised above. Laminar extrafloral nectaries on abaxial surface only, uncommon, mostly in the proximal half of the lamina, ± round, ca. 0.25 mm wide, green to black. Male inflorescences unknown. Female inflorescences not seen with flowers, apparently cymes, 1–3 in leaf axils of young stems, each 1–3-flowered, though no more than a single fruit seen on any inflorescence, axes subterete, moderately to densely strigillose, **fruiting peduncle** 0.5–2 mm long; **fruiting pedicel** 1.5–5 mm long, with a 4-angled pyramidal apex jointed to the receptacle within the basal protuberance of the calyx, subtended by 2–3 lanceolate bracts, ca. 2mm long. Female flowers unknown, except the style at least 2.4 mm long and 0.5 mm wide, hairy, the hairs off-white to reddish, up to 0.7 mm long, ± straight, ± terete, divided into two appressed, ascending branches at least 0.7 mm long (style details based on those persisting on fruit). Fruiting calyx thick, but not fleshy, exterior moderately strigillose, the epidermis viscid, **tube** patent, with a basal protuberance 1.3-2 mm long, 6-7.5 mm wide between opposing sinuses, interior with numerous minute, reddish hairs, lobes 4–5, reflexed, roundish, the margins weakly revolute, 4–6 mm long, 4–8 mm wide, interior glabrescent, viscid. Fruit ovoid-ellipsoid, often asymmetric, (15–)18–24 mm long, (11-)13-15(-17) mm in diameter; hairy near the apex, sometimes with hairs similar to those of the style scattered over the distal third, locules unknown, probably 1–4; flesh unknown; epidermis ± smooth, yellow to orange in life when mature, brownish yellow in herbarium material; seeds not observed, loosely contained (audibly so) in the locules of dried specimens.

Two of the paratypes (A. Campos V. 1017, MO and A. Campos V. & R. Torres C. 825, MO) were originally identified as D. campechiana, but annotated by R. Durán "No es Diospyros campechiana" in 1995. These specimens were later identified as D. campechiana by B. Wallnöfer in 1999. While this species is clearly a



FIG. 4. The holotype of *Diospyros camposii*. A. Fruiting branchlet. B. Fruiting inflorescences.

close relative of *D. campechiana*, that taxon is found primarily in lowland tropical forests associated with wetlands and riparian areas of major river systems between sea-level and 270 m elevation in the states of Tabasco, Campeche, Chiapas, and Veracruz, Mexico, and Guatemala, while *D. camposii* has been found only in Oaxaca in cloud forest between 1200 and 1550 m elevation. There is approximately a 300 km disjunction from the nearest populations of *D. campechiana* in the coastal lowlands of Veracruz to the mountains in Oaxaca where *D. camposii* occurs.

Diospyros camposii can be separated from D. campechiana by its shorter, widely ovate to elliptic lamina with a minutely ridged, but not at all revolute, margin. Although sometimes elliptic, the lamina of Diospyros campechiana is typically longer and more oblong in outline, and the margin is distinctly revolute. While both species are strigillose, D. camposii lacks the additional hirtellous vestiture always present in D. campechiana. Diospyros camposii also has a larger, thicker, fruiting calyx, with reflexed sepal lobes, in contrast to the thinner calyx with spreading lobes of D. campechiana. Finally, the fruits of D. camposii are longer and have a hairy apex, with the pubescence extending onto the style. The fruits and style of D. campechiana are glabrous. Distribution and ecology.—This species is currently known only from a small area on the Pacific Slope of the Sierra Madre del Sur (Fig. 5), where it is reported to occur in cloud forest (bosque mesófilo) in association with Alnus acuminata, Arbutus xalapensis, Chiranothodendron pentadactylon, Clethra mexicana, Cornus disciflora, Dendropanax arboreus, Ficus pertusa, Inga eriocarpa, Ocotea helicterifolia, Oreopanax xalapensis, Ormosia oaxacana, Parathesis brevipes, Picramnia lindeniana, Quercus candicans, Siparuna andina, Ulmus mexicana, Viburnum elatum and Zinowiewia integerrima (Campos-Villanueva & Villaseñor 1995). The area has a large number of canyons with permanent streams, and soils consisting of a deep layer of organic matter over red clay (Campos-Villanueva and Villaseñor 1995). The holotype was collected in pine-oak forest.

Etymology.—This species is named in honor of the Mexican botanist Alvaro Campos-Villanueva, who collected the holotype, and participated in all known collections of the species. He is also an author of a flora of the Municipio de San Jerónimo Coatlán in the Sierra Madre del Sur.

Specimens examined. **MEXICO. OAXACA. Mpio. San Jerónimo Coatlán:** 41 km al SW de San Jerónimo Coatlán, cañada de bosque mesófilo, suelo amarillo arcilloso, 16° 10'N, 96° 58'W, 1250 m, 17 Jan 1988, *A. Campos V. 1017* (MO); 12.3 km al N de Piedra Larga, sobre el camino a Progreso, la desviación se encuentra 9.6 km al NE de Piedra Larga, carr. a Miahuatlán, bosque mesófilo en bosque de pino, en cañada, 16° 09' 00"N, 97° 01' 00"W, 1200 m, 16 Dec 1987, *R. Torres C. & A. Campos 10895* (MO). **Mpio. Piedra Larga:** 12.5 km al NE de Piedra Larga, sobre el camino a El Progreso, bosque mesófilo, suelo negro, 16° 10'N, 97° 01'W, 1300 m, 15 Dec 1987, *A. Campos V. & R. Torres C.* 825 (MO).

Diospyros crotalaria M.C. Provance & A.C. Sanders, sp. nov. (Figs. 1b, 1d, 6, 15a). Type: COSTA RICA. PUNTAR-ENAS. Cantón de Osa: R.F. Golfo Dulce, Península de Osa, Rancho Quemado, Sector Oeste, 08°, 41' 10"N, 83° 35' 10"W, 400 m, 9 Sep 1992, J. Marín 512 (HOLOTYPE: MO-5316690!; ISOTYPES: CR, K!).

Arbor *D. harmanniana* S. Knapp similis, sed lamina oblonga usque oblongo-obovata, fructu glabrato, stylibus glabratis, gracilioribus, erectibusque et divisis prope usque basum, calycis fructiferis gracilibus, lobis reflexis differt.

Trees 10–20 m tall, probably evergreen; **trunk** recorded up to 15 cm dbh, bark reportedly thick; **young stems** reddish brown, somewhat compressed, shallowly channeled, or with some minor furrows, glabrescent to sparsely strigillose, the hairs pale yellow to dark red or nearly black; **mature stems** terete, rugose, densely lenticellate. **Leaves** alternate, simple, entire; **petioles** 4-9(-10) mm long, subterete, epidermis often scintillant, atropurpureous, rugulose, the wrinkles often transverse, sometimes developing into fissures; glabrous to sparsely strigillose, the hairs slightly flexuose, ascending, and pale yellow, or straight, appressed, and dark red to nearly black; shallowly V-grooved above, the groove sometimes with an additional narrow channel down its center, glabrous below, sometimes with a few small longitudinally oriented lenticels; **lamina** subcoriaceous, oblong to oblong-obovate, sometimes narrowly ovate, 74–150 mm long, 26–49 mm wide, length to width ratio ca. 2.5–3 : 1, *base* acute to subacute, *margin* flat, *apex* acuminate with a rounded tip; **lower lamina surface** reddish brown, slightly darker than above, dull, glabrescent or with scattered minute, 0.2–0.5 mm long, straight, appressed, dark red to nearly black, sometimes pale yellow



Fig. 5. Distribution of Diospyros camposii and D. campechiana in Mexico and Guatemala.

dark and recessed, **upper lamina surface** grayish green, not glossy, though slightly more shiny than below,

glabrous, epidermis densely papillose, the papillae angular. Venation eucamptodromous; midrib narrow but prominently raised below, rounded, longitudinally wrinkled, glabrate to sparsely strigillose; shallowly V-grooved above, glabrous; lateral veins 6–9(–10) per side, fine, raised below, forming inconspicuous loops with superadjacent laterals, flush or slightly depressed above, papillae absent; 3° veins fine, inconspicuously raised below, imperceptible above, or barely so, and then depressed. Laminar extrafloral nectaries on the abaxial surface only, relatively common, round to elliptic, 0.2–0.5 mm wide, black. Male inflorescences unknown. Female inflorescences cymes, 1 per leaf axil on young stems, 1-2-flowered, producing 1-2 fruit, axes ± terete, densely strigillose, the hairs flexuose, pale yellow to dark reddish brown, subtended by 2-3 opposite pairs of strigillose, persistent, deltoid bracts; fruiting peduncle 0.5-1.5 mm long; fruiting pedicel 1–2 mm long, with a 1 mm long 4-angled apex that forms a joint within the basal protuberance of the calyx. Female flowers unknown, except styles (2) erect, divided ± to the base, 4-angled, at least 0.9 mm long, 0.2 mm wide, essentially glabrous, though a long solitary hair was seen in the style branch fork on two of the known fruit (style details based on remnants from fruit). Fruiting calyx relatively thin (not fleshy), reportedly green in life, drying very dark, exterior strigillose, the hairs pale yellow to dark red, epidermis viscid, tube patent, with a ca. 1.5 mm long basal protuberance, 5–6 mm wide between opposing sinuses, interior sometimes with numerous minute, reddish hairs, lobes 4–5, usually reflexed, ovate, 2.4–3 mm long, 3-4 mm wide, the margins flat to weakly revolute, with a few cilia near the sinuses, moderately pubescent inside, the hairs minute, appressed, pale yellow to dark red. Fruit glabrous, 13-19 mm long, 15-20 mm wide, depressed globose to subglobose, often appearing 2-4 lobed (when dry) due to conformation of the fruit wall to the shape of the (1–4) locules with developing ovules; **flesh** exiguous; **epidermis** smooth, yellow in life when nearly mature, drying orangish-brown, red when mature, drying dark reddish brown; seeds 1–4, brown, loosely contained in the fruit, ± ellipsoid, 9–11.5 mm long, with 1 or 2 flat surfaces, ca. 6 mm wide, dorsal surface broadly convex, with a prominent vascular strand, texture rugulose-foveolate.

Specimens examined. COSTA RICA. PUNTARENAS. Cantónde Osa: R.F. Golfo Dulce, Península de Osa, Cerro Chocuaco, camino el



FIG. 6. The holotype of *Diospyros crotalaria*. A. Fruiting branchlet with persisting calyces. B. Fruits.

faro, 08° 43' 20"N, 83° 32' 20"W, 400 m, 28 Dec 1993, *R. Aguilar* 2877 (CR, K!, MO!). Cantón de Golfito Jiménez: Dos Brazos de Río Tigre, Cerro Müeller (falso Müeller) hasta Cerro Rincón, siguiendo el sendero entre las quebraditas (following the path between the small creeks), 08° 30' 35"N, 83° 28' 15"W, 782 m, 25 Nov 1990, *G. Herrera* 4647 (CR, K!, MO!).

The specimens of *D. crotalaria* we examined had not previously been determined to species. *Diospyros crotalaria* is similar to *D. hartmanniana*, but can be separated (Table 1) by its oblong lamina, glabrous fruits, and more slender, glabrous, erect styles, which are divided nearly to the base. Furthermore, *D. crotalaria* has a thinner calyx, and smaller, reflexed calyx lobes.

Distribution and ecology.—Apparently endemic to hills and canyons with wet tropical evergreen forest between 400 and 800 m elevation on the Osa Peninsula on the coast of southwestern Costa Rica (Fig. 14). Reports of *D. hartmanniana* from the Osa Peninsula (e.g., Zamora et al. 2004) may have been in reference to this species. The closest population of *D. hartmanniana* to the Osa Peninsula, that we know of, is about 75 km southeast in Panama.

Etymology.—This species is named for the rattling noise of the seeds in the locules of fruit on herbarium specimens.

Diospyros haberi M.C. Provance & A.C. Sanders, sp. nov. (Figs. 7, 15d). Type: COSTA RICA. ALAJUELA. Cantón de Upala: P. N. Rincón de la Vieja, Cordillera de Guanacaste, sendero La Siembra, c. a 7 km de la casa de Administración, 10° 47' 50"N, 85° 18' 19"W, 1500 m, 6 Jul 1991, *G. Rivera 1422* (HOLOTYPE: MO!; ISOTYPES: K!).

Arbor *D. hartmanniana* S. Knapp similis, sed lobis calycorum adaxialles prope glabratis, 1.5–2 mm longis, apico laminae rotundo, superficio laminae superioris olivaceo, splendiore clarioreque quam superficio inferioris olivaceo-griseo, uno (raro duobus) style glabrato differt.

Trees 8–28 m tall, apparently evergreen; **trunk** up to 60 cm dbh, the bark reportedly black with white patches; young stems 4–5 angled, somewhat compressed and channeled, sulcate, shiny, minutely black gland-dotted, sparsely strigillose; mature stems terete, glabrate, the epidermis light to dark green, smooth to half-netted, eventually lenticellate. Leaves alternate, simple, entire; petioles 3.5–9 mm long, ± terete, epidermis light green to castaneous or atropurpureous, shiny, sometimes transversely fissured, rugulose below, glabrous to sparsely strigillose, rounded above, rugulose and sparsely strigillose, channeled, often deeply, glabrous within or with scattered black hairs; lamina subcoriaceous, elliptic, 30–96 mm long, 17–40 mm wide, length to width ratio ca. 1.8–2.7: 1, base acute to attenuate, margin flat, though thickened, apex acute to obtuse, rarely slightly acuminate; lower lamina surface greenish to grayish brown, glabrate to sparsely strigillose, guard cells often dark, the stomatal apparatus often recessed; upper lamina surface greenish brown, shinier and slightly lighter than the lower surface, glabrate, epidermis markedly papillose, the papillae angular. Venation brochidodromous to eucamptodromous; midrib narrow below, subprominent, glabrate to sparsely strigillose, epidermis often darkened, longitudinally wrinkled, shallowly V-grooved above, glabrous or with some scattered dark appressed hairs; lateral veins 6–9 per side, fine, raised below, barely raised above; 3° veins slightly raised below, inconspicuous above. Laminar extrafloral nectaries on the abaxial surface only, usually near the midrib and towards the base, round to elliptic, 0.1–0.3 mm wide, dark green to dark brown. Male inflorescences solitary compact cymes in leaf axils of young stems, (1–)2–3-flowered, 6 mm long, axes 4-angled, strigillose, subtended by 1–2 pairs of deltate, 0.7 mm long, 0.6 mm wide bracts; peduncles 0.3 mm long; pedicels 0.3–0.8 mm long. Male flowering calyx crateriform to subrotate, exterior drying dark greenish brown, 3 mm wide, tube 1.5 mm long, exterior sparsely black strigillose, interior unknown, lobes 4, widely ovate, 0.5 mm long, 1–1.3 mm wide, erect, exterior glabrate to sparsely black strigillose, margins densely ciliate, interior glabrous; male corolla white in life, drying dark brown, glabrous, tube urceolate, 2 mm long, 2.6 mm wide, lobes 4, quadrate, 1.4 mm long, ca. 1.4 mm wide; only three flowers were seen, none were dissected, thus stamen morphology is unknown, except that anthers have a slender, tapering connective. Female inflorescences solitary, subsessile flowers in leaf axils of young stems, or rarely 2-flowered compact cymes, but no more than a single fruit seen in an inflorescence; axes 4-angled, sparsely strigillose, with 1–2 pairs of persistent, ovate bracts, 0.8 mm long, 1 mm wide; fruiting peduncles 0–0.5 mm long; fruiting pedicels ca. 0.5 mm long, with a 0.3 mm long



Fig. 7. Diospyros haberi. A. Leaves and male flower (W. Haber & S. Daniel 9895, MO). B. Branchlets with immature fruits (from the holotype). C. Female flower bud (G. Rivera 1422, K). D. Detail of immature fruits (from the holotype). E. Male inflorescence (W. Haber & S. Daniel 9895, MO).

TABLE 1. Morphological comparison of species of the Diospyros campechiana complex in Costa Rica and Panama.

	D. panamense	D. hartmanniana	D. crotalaria	D. haberi	
Fruiting calyx	thick	thick	thin	thick	
Fruiting calyx tube width (distance between opposing sinuses)	7–10 mm	5–6 mm	5–6 mm	5.1–6.6 mm	
Fruiting calyx lobe length Fruiting calyx lobe width	2.7–5 mm 4.5–9 mm	2.7–3.8 mm (4–)4.4–5.5 mm	2.4–3 mm 3–4 mm	1.5–2 mm 3.8–5.3 mm	

Fruiting calyx lobes

Fruit length Fruit vestiture

Style

Stem, petiole and midrib

Lamina shape

 \pm spreading spreading to slightly reflexed (14 -)17 - 20 mmup to 33 mm glabrous when usually hairy, especially at the mature, hairy at apex and base when immature 1, hairy, minutely deltoid-bifid minutely curvedacicular pubescent oblong-elliptic to elliptic, apex acuminate

base and apex 1, hairy, divided nearly to the base, spreading in the form of a 'V' not curved-acicular pubescent elliptic, apex acuminate

2, \pm glabrous, divided to the base, parallel and erect not curved-acicular pubescent oblong to oblongobovate, sometimes narrowly ovate, apex acuminate

reflexed

13–19 mm

glabrous

 \pm spreading

14 - 18 mmglabrous when mature, hairy at apex immature

1(-2), glabrous, shortly deltoid-bifid, often cleft on one side not curved-acicular pubescent elliptic, apex

rounded

Lamina size	(96–)127–240 mm	(50–)64–163 mm	74–150 mm long,	30–96 mm long
	long, 45–107	long, 25–70	26–49 mm wide	17–40 mm wide
	mm wide	mm wide		

4-angled pyramidal apex forming a joint within the basal protuberance of the calyx. Female flowers known from a single flower bud and style remnants on immature fruit. Female flowering calyx subcampanulate prior to anthesis, sparsely strigillose, 6.3 mm wide, tube 2.5 mm long, lobes (3–)4, thick (ca. 0.8 mm at 1/4 length), \pm evenly tapered to the apex, depressed-orbicular, 1.2-1.8 mm long, 3.9-4.1 mm wide, sometimes emarginate, asymmetric (hooking left viewed abaxially), ciliate on the left margin; female flowering corolla drying dark brown, tube ca. 2.2 mm long, with some scattered dark two-armed hairs, lobes 4, ca. 1.3 mm long, shape and width indiscernible, with some indistinct papillae; **pistil** unknown; **styles** 1(-2), 0.8–1.2 mm long, 0.7–1 mm wide, angular, bifid, the branches short, 0.2–0.3 mm long, deltoid, style often grooved on one side, rarely notched apically or grooved on both sides, glabrous, though strigillose near the base on the apex of the fruit (style and stigma [see below] details based on those persisting on fruit); stigmas depressed orbicular, 0.3 mm long, 0.7 mm wide; staminodes unknown. Fruiting calyx barely accrescent, thick, probably fleshy and green in life, drying brown to black, exterior sparsely strigillose, tube patent, with a basal protuberance 1.2–1.5 mm long, 5.1–6.6 mm wide between opposing sinuses, interior glabrous, or with some scattered reddish hairs, lobes ± spreading, depressed orbicular, 1.5–2 mm long, 3.8–5.3 mm wide, margins flat to slightly reflexed, ciliate, glabrous inside. Fruit 14–18 mm long, 10–20 mm wide, depressed globose to subglobose, often appearing 2–4 lobed when dry due to conformation of the fruit wall to the (1-4) locules with developing ovules, glabrous except for some dark hairs at the apex in immature fruit; flesh sparse, reddish, translucent and vitreous when dry; epidermis green in life when immature, becoming orange to red when mature, delicate, golden brown to dark reddish brown and loosely wrinkled when dry; seeds 1–4 (based on fruit lobes), reddish brown, loosely contained in the fruit, probably

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wedge-shaped, 14–18 mm long (width indeterminable, and shape uncertain, as the only seed observed had been sectioned longitudinally), surface texture rugulose in a maze-like pattern.

Distribution and ecology.—This species is associated with moist and windswept forests between 1100 and 1700 m elevation on the Pacific slopes of the Cordilleras de Guanacaste, Tilarán, and Talamanca, in Costa Rica (Fig. 14). Populations occur near, but as far as known do not overlap, populations of *D. hartmanniana* in the former two mountain ranges. All of the specimens examined had been recently identified as *D. hart-manniana*, to which it is doubtless closely related. The most obvious differences between the species (Table 1.) involve leaf apex shape, and style number and morphology. In addition to these characters, the interior of the sepal lobes in male and female flowers of *D. haberi* are glabrous, while in *D. hartmanniana* they are densely dark strigillose. The color and brilliance of the lamina is also different in these species. In *D. haberi* the greenish brown upper surface of the lamina is shinier and slightly lighter than the greenish to grayish brown lower surface. Brilliance is reversed in *D. hartmanniana*, where the grayish brown upper surface is duller than the reddish brown lower surface.

Etymology.—This species is named in honor of William A. Haber, a biologist who has contributed greatly to our knowledge of the biota of Costa Rica and who has documented the presence of this new species at Monteverde.

Specimens examined. **COSTA RICA. GUANACASTE. Cantón de Tilarán:** Cañitas, Río Cañas, Lado Pacifico, 10° 20'N, 84° 51'W, 1200 m, 25 Aug 1989, *E. Bello 1124* (MO). **PUNTARENAS. Cantón de Buenos Aires Olán:** siguiendo filas en cuenca superior de Río Cabagra, 9° 17' 40"N, 83° 11' 50"W, 1700 m, 24 Sep 1989, *G. Herrera 3542* (MO). **Cantón de Osa:** San Luis, Monteverde, Buen Amigo, 10° 16' 00"N, 84° 49' 00"W, 1100 m, 10 Nov 1993, *Z. Fuentes & E. Fuentes 565* (MO). **Cantón de Puntarenas:** Monteverde, Bajo Tigre Reserve, 10° 18'N, 84° 48'W, 1200–1300 m, 3 Apr 1991, *W. Haber & W. Zuchowski 10600* (MO); Monteverde, above Quebrada Máquina, along Fonseca, Hotel de Montaña and Savage Farms, 10° 18'N, 84° 48'W, 1100–1300 m, 3 Jun 1990, *W. Haber & S. Daniel 9895* (MO).

Diospyros hartmanniana S. Knapp, Novon 7:256. 1997. (Figs. 8, 9, 15e). Type: PANAMA. CHIRIQUÍ: near Coast Rican border, ca. 13 road-km from Río Sereno, Finca Hartmann, 1550–1750 m, 08° 50'N, 82° 45'W, 23 Oct 1992, G. McPherson &

P.M. Richardson 15959 (HOLOTYPE: BM; ISOTYPES: MO, PMA).

Trees 7–20 m tall, rarely a 1.5 m tall shrub, apparently evergreen; trunk up to 72 cm dbh, bark smooth and black, wood oxidizing bright yellow; young stems angular, often compressed, sulcate to channeled, shiny, often minutely black gland-dotted, glabrous to sparsely strigillose; mature stems dark, terete, smooth, glabrate to sparsely hairy, later half-netted, scaly and lenticellate. Leaves alternate, simple, entire; petioles 4–10 mm long, subterete, epidermis castaneous to atropurpureous, sometimes transversely fissured, sometimes scintillant, longitudinally wrinkled to colliculate below, shiny, glabrous to strigillose; glabrous above, markedly channeled; lamina subcoriaceous, elliptic, (50–)64–163 mm long, 25–70 mm wide, length to width ratio ca. 2-3: 1, base acute to attenuate, margin flat, though slightly thickened, apex acute to subacute, rarely obtuse, acuminate, the tip rounded; lower lamina surface reddish brown, glabrate to sparsely strigillose, aggregates of opaque off-white excrescences sometimes present, guard cells often dark and the stomatal apparatus often recessed; upper lamina surface grayish brown, duller than the lower surface, glabrous, epidermis conspicuously papillose, the papillae angular. Venation brochidodromous to eucamptodromous; midrib narrow below, though prominently raised, rounded, longitudinally wrinkled, glabrous to strigillose, the hairs pale or dark; V-grooved above, glabrate; lateral veins 6–11 per side, fine, raised below, slightly raised to barely depressed above, lacking papillae; 3° veins slightly raised below, indiscernible above. Laminar extrafloral nectaries on the abaxial surface only, common near the midrib and the base of the lamina, 0.1–0.5 mm wide, castaneous. Male inflorescences solitary compact cymes in the leaf axils of young stems, or several near the base of young stems, (1–)3–7-flowered, 7–11 mm long, axes 4-angled, densely reddish brown to black strigillose, subtended by several lanceolate to widely ovate, 1–2 mm long, ca. 1 mm wide bracts; peduncles 0.5–1.5 mm long; pedicels 0.5–1.5 mm long. Male flowers known only from buds. Male flowering calyx subrotate, with a basal protuberance ca. 1 mm long, exterior drying dark greenish brown, moderately strigillose, interior densely strigillose, 3.5–4.1 mm in widest dimension, tube 1–1.2 mm long, lobes 4–5, ovate, 0.9–1.2 mm long, 1.3–1.6 mm wide, suberect to spreading, margins ciliate; male corolla white to cream in life, drying dark brown, thick, glabrous, papillate, tube urceolate,

FIG. 8. Diospyros hartmanniana. A. Fruiting branchlets with persisting calices (G. Herrera 5669, K). B. Fruiting inflorescences (E. Bello 1767, MO). C. Immature fruits (E. Bello 2442, MO).

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Fig. 9. Diospyros hartmanniana (R. Espinoza et al. 884, MO). A. Male flower (sinus membranes torn). B. Mature male flower bud. C. Stamens.

1.6–2.8 mm long, 3.2–4.5 mm wide, lobes 4–5, widely ovate, 2.1–3.1 mm long, ca. 3 mm wide; stamens ca. 27 (based on R. Espinoza et al. 884 (MO) from Costa Rica) adnate to the base of the corolla, the filaments fused most of their length into ca. 13 pairs, comprised of inner and outer members (Knapp [1997] reports 10-12(-20) stamens, and illustrates 14 stamens in pairs based on McPherson & Hensold 15303 (MO) from Panama), anthers cream, the inner anthers often larger than the outer, lanceolate, (2.5)3–3.2 mm long (including connective), golden to reddish sericeous along the connective on both sides, the apex (connective) rostrate, slightly constricted basally, minutely muricate, filaments 1.2-1.5 mm long (fused portion of the filament pair), glabrate, free portion of the filaments 0.5–0.7 mm long, densely hairy, the hairs minute and curly; pistillode obturbinate, 1.4 mm high, 1.2 mm wide, ca. 8-lobed/grooved, the 'lobes' narrower than the 'grooves', presence of style-like structures indeterminable due to a dense vestiture of 0.5 mm long, red, flat, twisting hairs in the upper half. Female inflorescences unknown with flowers, apparently a 1–3-flowered compact cyme in leaf axils of young stems, with 1-2 fruit developing per inflorescence, axes \pm 4-angled, strigillose, with ca. 2 pairs of persistent, widely ovate bracts, 1.2–1.8 mm long, ca. 1.5 mm wide; fruiting peduncles 0–1.8 mm long; fruiting pedicels 0.5–2 mm long, with a 1–1.5 mm long 4-angled pyramidal apex, the distal 1/2 forming a joint within the basal protuberance of the calyx. Female flowers unknown, except style divided nearly to the base, branches angled away from one another in the form of a 'V', each 0.7–1.3 mm long, ca. 0.5 mm wide, densely reddish brown strigillose basally and where the style branches diverge (style and stigma [see below] details based on those persisting on fruit), stigmas minute, deltoid. Fruiting calyx thick, probably fleshy, reportedly brown in life, drying dark brown to black, exterior strigillose, the hairs pale yellow to dark, sometimes glabrescent, epidermis viscid, interior densely strigillose, tube patent, with a basal protuberance ca. 1.5 mm long, 5–6 mm wide between opposing sinuses, **lobes** 4–5, spreading, ovate, 2.7–3.8 mm long, (4–)4.4–5.5 mm wide, the margins flat, sparingly ciliate. Fruit (14–)17–20 mm long, (12–)17–20 mm wide, depressed globose to subglobose, often appearing 2–4 lobed when dry due to conformation of the fruit wall to the (1-4) locules with developing ovules, usually strigillose basally and at the apex; flesh sparse, reddish; epidermis smooth to wrinkled, in life orange to orangish red when mature, light brown to dark reddish brown when dry; seeds 1-4, loosely contained in the fruit, \pm wedge-shaped, reddish brown and rugulose-foveolate textured, though only immature seeds were seen. Distribution and ecology.—This species is associated with cloud and moist forests between 500 and 2200 m elevation, on slopes of the Cordilleras de Guanacaste and Tilarán in Costa Rica, and Talamanca (La Amistad) in Panama (Fig. 14). Populations occur near, but as far as known do not overlap, populations of D. haberi in the former two mountain ranges.

Collections examined. **COSTA RICA.** ALAJUELA. **Cantón de San Carlos:** La Fortuna, Finca El Jilguero, 10° 26' 35"N, 84° 41' 25"W, 1140 m, 27 Nov 1992, *G. Herrera 5669* (K). **Cantón de San Ramón:** Res. Biol. Monteverde, Valle del Río Peñas Blancas, Fila de Toro, Sendero Pipilacha y Capo Tres, [acca. W3 Tropicos 10° 18' 00"N, 84° 43' 12"W], 900–1100 m, 21 Jan 1991, W. *Haber (ex E. Cruz) 10632* (MO); Res. Biol. Monteverde, Estación Eladio's, 10° 19'N, 84° 43'W, 820 m, 2 Oct 1990, *E. Bello 2442* (MO). **Cantón de Upala:** P.N. Rincón de la Vieja, Cordillera de Guanacaste, sendero a la Quebrada Mora, camino a la Colonia Blanca, 10° 46' 32"N, 85° 15' 10"W, 840 m, 30 Nov 1990, *G. Rivera 920* (K, MO); P.N. Guanacaste, Cordillera de Guanacaste, Estación, San Ramón, Dos Ríos, Sector La Campana, 10° 52' 50"N, 85° 24' 05"W, 550 m, 1 May 1993, *R. Espinoza et al.* 884 (K, MO); **Guanacaste. Cantón de La Cruz:** De Bahia Salinas a Santa Cecilia Hda. El Oro, 10° 59' 26"N, 85° 25' 40"W, 500 m, 5 Sep 1922, *R. Espinoza 531* (K, MO); **PUNTARENAS. Cantón de Coto Brus:** Zona Protectora Las Tablas, Cuenca Térraba-Sierpe, 08° 58' 42"N. 82° 50' 14"W, 1500–2000 m, 1 Nov 1996, *A. Rojas & E. Navarro & E. Alfaro 1757* (MO). **Cantón de Osa:** Reserva Biológica Monteverde Quebrada Veracruz, Finca Pablo Morales, 10° 15'N, 84° 48'W, 1600 m, 11 Jan 1990, *E. Bello 1767* (MO); San Luis, Monteverde, Cerro Banquete, camino a Surtubal, 10° 15' 25"N, 84° 47' 20"W, 1100–1200 m, 22 Mar 1994, *Z. Fuentes 704* (MO). **PANAMA. CHIRIQU.** Near border with Costa Rica, ca. 13 road km from Río Sereno, Finca Hartmann, 08° 50'N, 82° 45'W, 1400–1800 m, 12 May 1991, *G. McPherson & N. Hensold 15310* (B, 2 sheets, CAS); ridges leading to Cerro Pelota, Parque Nacional Amistad, 08° 52–53'N, 82° 44'W, 1700–2200 m, 21 Aug 2000, *S. Knapp & A. Monro* 9254 (MO).

Diospyros juruensis A.C. Smith, Brittonia. 2:163. 1936. (Figs. 10, 11). Type: BRAZIL. AMAZONAS: on varzea land, near mouth of Rio Embira (tributary of Rio Tarauaca), 7° 30'S, 70° 15'W, 26 Jun 1933, B.A. Krukoff 5003 (HOLOTYPE: NY; ISOTYPES: F, MICH, MO!).

A lengthy description here of the species based on the single sheet with male flowers we have seen seems premature to us. The characters that lead us to believe that *D. juruensis* belongs to the *D. campechiana* complex

B. A. ERUKOFP'S ISL EXPEDITION TO BRAZILIAN AMAZONIA BARN OF HIG FORUS 5003 Diopyron junnemsis A.C.S. Type collection June 26, 1933. State of Ameronas; near mouth of Rio Embira (tributary of Ris Tarmunca), lat. 7" 38' S., long. 76" 15' W. Speciments distributed through the New York Botanical Cardon

Fig. 10. The isotype of Diospyros juruensis (B.A. Krukoff 5003, MO). A. Fruiting branchlets with male inflorescences. B. Detail of male inflorescence.

FIG. 11. The isotype of Diospyros juruensis (B.A. Krukoff 5003, MO). A. Pistillodes. B. Stamens.

include the large oblong-oblanceolate leaves with frequent darkened guard cells and somewhat recessed stomatal apparatus; male inflorescence axes that are markedly 4-angled; depressed orbicular male calyx lobes; a lobed pistillode (Fig. 11a) very similar to that seen in *D. campechiana* (Fig. 3b); stamens adnate to the base of the corolla, fused near the base of their filaments into ca. 16 pairs, outer and inner stamens \pm same length, densely golden sericeous on the filament and connective, anthers reddish orange, lanceolate, the apex (connective) tapered and minutely muricate.

Diospyros panamense S. Knapp, Novon 9:524. 1999. (Figs. 12, 13, 15f). Type: PANAMA. SAN BLAS: Río Diablo y vecinidad de Duque Sui, a unos 10 km de la costa frente a la Isla de Nargana, ruta hacia Cerro Ibedón, 80–110 m, 09° 22'N, 78° 35'W, [1 Jul 1992 acc. to W3Tropicos], H. Herrera et al. 1175 (HOLOTYPE: BM; ISOTYPES: MO, PMA). Replaced name: Diospyros whitei S. Knapp, Novon 7:258. 1997. Non Diospyros whitei Dows.-Lem. & Pannell, Bull. Jard. Bot. Nat. Belg. 65:399. 1966.

Trees 5–20 m tall, evergreen; trunk up to 40 cm dbh, bark black, wood reportedly soft; young stems hollow, distally angular, ± compressed and shallowly channeled, terete and smooth proximally, dark, green, brown or gray, occasionally sparsely strigillose, the hairs dark, or sometimes yellowish, minutely pubescent, the hairs colorless, curved-acicular, ca. 0.03 mm long; mature stems with thick, scaly, gray to dark brown bark, lenticels prominent, stemwood reddish brown in stems ca. 10 mm wide. Leaves alternate, simple, entire; petioles 7–14 mm long, subterete, minutely curved-acicular pubescent, epidermis green or atropurpureous, sometimes glaucous and scintillant, sometimes with a few transverse fissures, rounded below, glabrate to sparsely strigillose, ± flattened above, sparsely strigillose, with a densely glandular narrow central channel; lamina subcoriaceous to coriaceous, oblong-elliptic to elliptic, though slightly wider in the upper half, (96–)127–240 mm long, 45–107 mm wide, length to width ratio ca. 2–2.6:1, base acute to obtuse, sometimes abruptly decurrent on the petiole, margin flat to revolute, apex acuminate with a rounded tip; lower lamina surface reddish brown, glabrate to sparsely strigillose, faintly papillose, guard cells sometimes dark and recessed; upper lamina surface grayish to greenish brown, markedly duller than the lower surface, glabrous to sparsely strigillose near the midrib, epidermis conspicuously papillose, the papillae angular. Venation eucamptodromous, subscalariform (sensu Knapp 1997), minutely curved-acicular pubescent below; midrib prominent below, rounded, glabrate to sparsely strigillose, longitudinally wrinkled, concave above, sparsely to moderately strigillose and glandular; lateral veins \pm evenly spaced, 6–9 per side, fine below, though prominently raised, barely depressed above, the surface smooth, and so, conspicuous adjacent to the papillate surface of the lamina; **3° veins** fine below, though prominently raised, scarcely, if at all apparent above. Laminar extrafloral nectaries on the abaxial surface only, occasional, more frequent near the midrib, dark brown to black, ca. 0.6 mm wide, minutely rimmed. Male inflorescences glomerules, or compact cymes, (3–)10–20-flowered, a few at the base of young stems, or solitary in leaf axils, axes 4-angled, dark reddish brown strigillose, subtended by ± 2 strigillose triangular bracts, ca. 0.9 mm long; peduncles 0.1–1

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Fig. 12. Diospyros panamense. A. Immature fruit (E. Alfaro 291, MO). B. Fruiting branchlets (R. Aguilar et al. 2727, MO). C. Male inflorescences (R. Aguilar 2749, K). D. Fruits (R. Aguilar et al. 2727, MO).

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Fig. 13. *Diospyros panamense* (*R. Aguilar 2749*, MO). **A.** Detail of male inflorescences with flower buds from fragment folder. **B.** Interior of male calyx with pistillode. **C.** Stamens.

mm long; **pedicels** 0–1.4 mm long. **Male flowers** known only from buds; **male flowering calyx** subrotate with a short basal protuberance, exterior drying dark brown to black, strigillose, interior densely strigillose, 3–4.2 mm in widest dimension, **tube** 1–1.5 mm long, **lobes** 4–5, depressed orbicular to ovate, 1–1.6 mm long, 1.8–2.4 mm wide, suberect nearing anthesis; **male corolla** white in life, drying dark brown, thick, glabrous, papillate, **tube** urceolate, 0.8–1.9 mm long, 2.6–3.2 mm wide, **lobes** 4–5, ovate, 1.4–2.2 mm long, 1.6–1.7 mm wide; **stamens** 24–28, adnate to the base of the corolla, fused near the base of their filaments into 12–14 pairs, outer stamens bowing inwards, outer and inner stamens ± same length, the outer stamen golden sericeous abaxially on the filament and connective, the hairs long and curved, also golden sericeous

on the connective adaxially and on both surfaces of the inner stamen, but the hairs shorter, anthers reddish orange, lanceolate, ca. 2 mm long, the apex (connective) tapered and minutely muricate, filaments 0.2–0.4 mm long; pistillode obturbinate, markedly 12–14-lobed, ± 1 mm wide, with 2–3 style-like apical structures, each with a few long straight golden hairs. Female inflorescences not seen with flowers, apparently a solitary 1–3-flowered compact fasciculate cyme in the leaf axil of young stems, though no more than one fruit per inflorescence observed, axes 4-angled, sparsely pale strigillose, subtended by several thin, deltoid, strigillose, persistent bracts, ca. 1.5 mm long; fruiting peduncles 0–1 mm long; fruiting pedicels 1–4 mm long, with a 1–1.2 mm long 4-angled apex, the distal 0.5 mm depressed-pyramidal, forming a joint with the receptacle within the basal protuberance of the calyx. Female flowers unknown, except style 1.3–1.6 mm long, 0.9–1.3 mm wide, hairy, the hairs pale, yellowish, slightly wavy, terete to slightly 4-angled, bifid, the branches short, 0.2–0.3 mm long, deltoid (style and stigma [see below] details based on those persisting on fruit), stigmas depressed orbicular, 0.3 mm long, 0.7 mm wide. Based on the holotype (which we have not seen), Knapp (1997) reported, "styles 5, 1–1.5 mm, fused at the base" and "stigmas irregularly lobed." Fruiting calyx thick, possibly fleshy in life, drying dark brown to black, exterior sparsely to densely strigillose, the hairs mostly pale, tube patent, with a short protuberance in immature fruit, this apparently absent at maturity, 7–10 mm wide between opposing sinuses, interior densely golden strigillose, **lobes** 4–5, spreading to slightly reflexed, depressed-orbicular, 2.7–5 mm long, 4.5–9 mm wide, the margins sometimes ciliate, interior sparsely golden strigillose. Fruit up to 33 mm long, 33 mm wide, globose to subglobose, immature fruit densely hairy near the base and the apex, the remainder sparsely hairy, the hairs golden to dark red, mature fruit glabrous, *locules* probably 1-4, small damaged fruits with ± 2 locules observed, and Whitefoord and Knapp (1998–onward) reporting "lóculos 4?"; flesh unknown in mature fruit; epidermis mature fruit loosely wrinkled, cracked and scaly near the base and apically, the largest fruits seen (R. Aguilar 2727 et al., MO) reportedly brilliant green; seeds unknown. Fruits are suspected to contain up to 4 seeds, though fruits in *E. Alfaro* 291 (MO), are probably 1 and 2-seeded based on the number of enlarged locules.

Distribution and ecology.—Lowland rain forests of Costa Rica, Panama, and possibly Columbia, between 80 and 1200 m elevation (Fig. 14). There are reports (Zamora et al. 2004) of this species from both near the highest peaks (617–745 m) and in the low forests (e.g., 0–300 m) on the Osa peninsula. However, we have not seen collections from either of these regions.

Specimens examined. COSTA RICA. PUNTARENAS. Canton de Osa: Fila Costeña, Río Piedras Blancas, junto a la casa, faldas Cerro Anguciana, Fila Cruces. 08° 49' 02"N, 83° 11' 23"W, 900 m, 9 Dec 1993, R. Aguilar et al. 2727 (MO, K); Fila Costeña, Río Piedras Blancas, cerca de la casa, Cerro Anguciana, Fila Cruces, 08° 49' 02"N, 83° 11' 23"W, 900 m, 10 Dec 1993, R. Aguilar 2749 (MO, K). SAN JOSE. Cantón de Perez Zeledon: Cordillera de Talamanca, La Nubes, Santa Elena, 09° 23' 30"N, 83° 35' 50"W, 1210 m, 3 Aug 1995, E. Alfaro 291 (MO). PANAMA. DARIEN: Cerro Pirre, 4 Aug 1967, N. Briston 1229 (MO-2 sheets).

KEY TO THE MESOAMERICAN SPECIES OF THE DIOSPYROS CAMPECHIANA COMPLEX

1. Fruits mostly globose to subglobose; plants of Panama and Costa Rica.

- 2. Styles 2 or 1 style divided nearly to the base (Fig. 15).
 - 3. Lamina oblong to oblong obovate; fruiting calyx thin (not fleshy), the lobes 3–4 mm wide, usually reflexed; fruit apex glabrous; styles 0.2 mm thick, erect, glabrous D. crotalaria
 - 3. Lamina elliptic; fruiting calyx thick (fleshy), the lobes 3.8–5.5 mm wide, spreading; fruit apex hairy; styles 0.5–1 mm thick, diverging from near the base in the form of a V' to \pm erect, hairy or glabrous.
 - 4. Lamina apex acuminate, upper lamina surface duller and slightly darker than reddish brown lower surface; fruiting calyx lobes 2.7–3.8 mm long, densely dark strigillose inside; style hairy, branches diverging from near the base in the form of a 'V'_ D. hartmanniana
 - 4. Lamina apex rounded, upper lamina surface shinier and slightly lighter than the greenish to grayish brown lower surface; fruiting calyx lobes 1.5–2 mm long, glabrous inside; style branches glabrous, \pm erect (This species typically has one style with some apical notches, or a groove down one side).

D. haberi

2. Style 1 (Fig. 15).

5. Fruiting calyx lobe 2.7–5 mm long, 4.5–9 mm wide; fruiting calyx tube 7–10 mm from sinus to opposite sinus; lamina 96-250 mm long, 45-107 mm wide, the apex acuminate; young stems, petioles, and

FIG. 14. Distribution of Diospyros crotalaria, D. hartmanniana, D. haberi and D. panamense in Costa Rica and Panama.

midribs with a sparse, minute, curved-acicular pubescence; fruits up to 32 mm long; style undivided, 1.5–1.6 mm long, 1–1.5 mm thick _______ **D. panamense**

- Fruiting calyx lobe 1.5–2 mm long, 3.8–5.3 mm wide; fruiting calyx tube 5.1–6.6 mm from sinus to opposite sinus; lamina 30–96 mm long, 17–40 mm wide, the apex rounded; young stems and midribs without a minute curved-acicular pubescence; fruits 14–18 mm long ______ D. haberi
- 1. Fruits mostly ovoid-ellipsoid; plants of Mexico and Guatemala.

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- 6. Stems, petioles, midribs, and inflorescences minutely hirtellous (in addition to being dark strigillose); fruit 13–17 mm long, the apex glabrous; style 1–2.1 mm long, glabrous; fruiting calyx thin, the tube 3.5–6 mm from sinus to opposite sinus, the lobes 2–4 mm long, not reflexed; lamina 100–285 mm long, oblong to oblong-lanceolate to elliptic, sometimes oblong-oblanceolate, the margins distinctly revolute — D. campechiana
- 6. Stems, petioles, midribs, and inflorescences not minutely hirtellous (dark strigillose only); fruit (15–)18–24 mm long, the apex hairy; style ca. 2.4 mm long, hairy; fruiting calyx thick, the tube 6–7.5 mm from sinus to opposite sinus, the lobes 4–6 mm long, reflexed; lamina 55–152 mm long, widely ovate to elliptic, the margins minutely ridged ______ D. camposii

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Fig. 15. Stylar variation in the *Diospyros campechiana* complex. **A.** Styles (with damaged apices) persisting on the fruit apex of *D. crotalaria*, based on the holotype. **B.** Branched style (with damaged stigmas) of *D. campechiana*, based on *W.E. Harmon & J.E. Fuentes 5790* (UMO). **C.** Branched style (with damaged apices, and second branch barely visible at this angle) of *D. camposii*, based on the holotype. **D.** Style with stigmas at fruit apex of *D. haberi*, based on *G. Rivera 1422* (K). **E.** Styles with minute stigmas (arrow) at the fruit apex of *D. hartmanniana*, based on *E. Bello 2442* (MO). **F.** Style with stigmas at fruit apex of *D. panamense*, based on *E. Alfaro 291* (MO).

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